SERUM GLUCOSE AND FREE FATTY ACIDS IN MAN DURING PROLONGED EXERCISE

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Running [illegible] metabolism during prolonged exercise in man

The theory that carbohydrates are the preferred source of energy for muscular activity has been historically accepted by physiologists. Because of the incomplete oxidation of fats in the body which results in the accumulation of intermediates, high rates of fat metabolism lead to undesirable consequences. For example, Christensen and Hansen (7) demonstrated decreased physical efficiency and decreased work capability during the course of a 1-1/2-hr period of exercise in three subjects who for several days had consumed a diet high in fat content. However, when consuming a diet consisting predominantly of carbohydrate, the subjects were able to exercise for approximately 4 hr without apparent adverse effects. Similarly, during periods of food deprivation when substantial quantities of body fat are used to provide fuel for the working muscles, diminished levels of the blood sugar, acidosis and associated dehydration appear to be the dominant metabolic factors responsible for a diminished tolerance for physical work, Henschel et al. (17).

However, the above theory is difficult to reconcile with other experimental findings. Specifically, the studies by Courtice and Douglas (9) with postabsorptive subjects suggest the preferential and efficient metabolism of fats during long sustained work. In effect, they demonstrated during the course of a 10-mile walk of approximately 2-1/2 hr duration that a) exercise distinctly reduces sugar (sucrose, fructose, glucose) tolerance and also that b) exercise, as compared with a subsequent resting period, reduces the urinary excretion of ketone bodies. The latter finding has been confirmed recently by Johnson and Passmore (19). Additional indirect evidence of the efficient use of fat

by the body is suggested by the demonstration that experimental rats fed a high fat diet survive longer during subsequent fasting and are capable of greater amounts of physical work than animals fed a high carbohydrate or high protein diet (27). Also, deprivation of food for 5 days increases the endurance capacity of experimental dogs (31).

More challenging, however, are the relatively recent reports demonstrating the prompt availability of body fat as a source of energy and its rapid oxidation by muscle. Fat utilization is related, apparently, to its level in the blood and also to the circulatory rate. Thus, in addition to an augmented rate of glucose metabolism during exercise (8,15 24), a substantial amount of energy is derived from the direct oxidation of fats. During aerobic work of 1-6 hr duration with fasting subjects, both arterial and venous blood samples show steadily increasing levels of free fatty acids (FFA) (2,16 25). Venous blood levels of FFA decline abruptly after work (25), whereas arterial blood samples show first a transitory rise, followed by a decline (16); momentarily, the utilization of fat apparently does not keep apace with its mobilization from body depots. In fasting men, Havel et al. (16) estimate that 41-49% of energy expenditure is derived from the direct oxidation of FFA during long sustained work; 25-26% of energy is derived from fat oxidation during resting conditions. Subsequent to the feeding of carbohydrate, only 5-10% of energy is obtained from the oxidation of fats. In contrast, studies with dogs suggest that during work (29), only 13% of the FFA is oxidized as compared with 21-31% under resting conditions (1).

The results obtained for short periods of heavy work are different. However, they are also somewhat more difficult to evaluate owing to the accumulation of lactic acid and the displacement of the blood bicarbonate reserves which a) distort the respiratory exchange ratios and therefore result in an unreliable estimate of the metabolites which are oxidized, and also, b) require modification in the interpretation of lipid turnover rate. Two studies by Carlson and co-workers (4,5) of the effect of exercise for 4-30 min agree in demonstrating transitory decreases in both the arterial and venous levels of FFA. On the other hand, during work of 40-60 min duration, the arterial blood level of FFA tends generally to rise (6,14). The apparent discrepancy between the results obtained during light and heavy work has been ascribed to an increased rate of fatty acid oxidation during heavy exercise and also to a simultaneous inhibition, of the release of FFA from tissues due to rising blood levels of lactic acid (23).

We are interested in examining metabolism during conditions of elevated fat and carbohydrate oxidation and during different steady-state conditions. Within that general framework, investigations have been undertaken to evaluate the metabolic responses of fasting subjects to prolonged physical work. Since the data of other researchers indicated extreme variability of FFA mobilization in relationship to the degree of physical exertion, it was thought desirable to reinvestigate the effect of physical exercise to a) determine the feasibility of establishing prolonged steady-state levels of the blood FFA and glucose during work, b) assess the degree of carbohydrate depletion during conditions of depressed levels of the blood sugar, c) determine the maximal rate

of FFA mobilization, and d) determine the influence of elevated levels of blood sugar during maximal lipid mobilization. From a theoretical point of view, the studies were considered necessary in order to define different steady states and thus to provide guidance for future studies of C^{14} turnover and exchange kinetics. From a practical point of view, the studies were of interest in determining whether the plasma FFA might serve as a useful index of performance capacity.

The present report deals with the responses of postabsorptive men during two prolonged periods of physical activity, i.e., at rest or during treadmill walking. Reports of other aspects of the study will be presented elsewhere.

METHODS

The data presented have been drawn from experiments with 20 volunteer male subjects varying in age from 22 to 40 years. They were selected on the basis of motivation, and general health which was judged from their medical history and the results of physical examinations and laboratory tests. For several months, the subjects were required to participate in a formal program of physical conditioning which consisted of 20 min of calisthenics followed by an uninterrupted 2-mile run. Initially, participation in the physical conditioning program was required daily; later, the exercises were given only three times weekly. Individual questionnaires revealed no bizarre eating habits; nevertheless, menus were distributed to the subjects to help them adjust their daily caloric intake and maintain satisfactory body weights. None of the subjects were obese or exceptionally thin; their physical characteristics are shown in Table 1.

Table 1

The subjects participated in two separate tests (exercising or resting) which were planned for a duration of 24 hr. In all cases, they arrived at the laboratory at 6:30 A.M. in the postabsorptive state, i.e., 12 hr following the last meal. After voiding, the subjects were weighed nude and then were required to lie quietly for 1 hr. Polyethylene catheters were inserted into one of the antecubital veins, stainless steel electrodes were applied to the chest, and a thermistor probe was inserted 4 in. into the rectum. Testing commenced at 8:30 A.M. During the test, blood and urine samples, rectal temperature, heart rate and blood pressure, and respiratory gas samples were taken every 1-1/2 hr. Each subject drank 300 cc of water every 1-1/2 hr, and took 1 g of salt every 4 hr.

The environmental conditions were selected to avoid heavy sweating which could result in important losses of body water and minerals. For studies of the resting state, the subjects rested quietly on a reclining couch for 24 hr in an air-conditioned room maintained at 75°F and 50% relative humidity. Noise level, air movement, and lighting were constant. Sleeping was not permitted. All studies of physical exercise followed a common plan of aerobic work on a treadmill in a room maintained at 68°F and 50% relative humidity. The speed of walking and grade were selected for each subject to provide a work load which was approximately 33% of the maximal work capacity. The speed and grade varied between 2.6-2.9 mph and from 0-3 degrees of incline, respectively. Each period consisted of 1 hr and 20 min of walking followed by 10 min of rest. This schedule was followed for a total of 24 hr or until the onset of fatigue.

Oxygen consumption and carbon dioxide production were determined from expired air samples collected through low-resistance connections in chain-compensated gasometers. Noseclips and mouthpieces were used in conjuction with standard high-velocity respiratory valves. During resting conditions, expired air samples were collected for 10 min; during exercise, collections were made for 4 min. Samples of expired air were analyzed for their content of O_2 and CO_2 with a Beckman oxygen analyzer and an LB-1 carbon dioxide analyzer, respectively. All respiratory volumes were computed for STPD conditions.

Heart rate was measured with a cardiotachometer. Body temperature was recorded through a multichannel telethermometer.

Blood samples were drawn from the indwelling catheters. Aliquots were set aside in heparinized capillary tubes for the determination of hematocrit; the rest was allowed to clot, and the serum drawn off and frozen for subsequent analyses for glucose (26,28), phosphorus (12), lactic acid (21), sodium and potassium (Baird Atomic flame photometer) nonprotein nitrogen (13), and FFA (11,30).

After urine volume was measured, all samples were frozen. Subsequently, they were examined for their content of nitrogen (20) and creatinine (3); ketone bodies were measured as acetone (22).

The statistical procedures set forth by Dixon and Massey (10) have been applied to all the data.

RESULTS

Maximal endurance capacity. Actual maximal walking time varied between 519 and 1281 min. The mean and median were 982 and 935 min,

respectively. Five subjects completed the full 24-hr session, whereas one subject stopped after approximately 9 hr. A comparison of the distribution function of our data with that obtained with normal random deviates showed that total walking times were not normally distributed over the 24-hr period of testing. The five subjects who completed the test complained largely of boredom; however, most of the subjects complained of fatigue and drowsiness, muscular soreness, and blisters. Hunger or nausea was noted only occasionally.

Physiologic responses. A comparison of the respiratory gas exchange, heart rate, body temperature, and the blood levels of NPN, lactate, sodium, potassium, and phosphorus in resting and working subjects is shown in Table 2. As is to be expected, the oxygen consumption, heart rate, and rectal temperature are significantly higher during work than during the resting state, $p < 0.05$. On the other hand, the respiratory quotient and the serum levels of NPN, lactate, sodium, potassium, and phosphorus were similar during both test conditions. There was no tendency for those values to vary systematically during the test.

Table 2

The variations in serum FFA and glucose during resting conditions are shown in Fig. 1. During the first 10 hr of observation, the serum level of glucose declined from an average initial value of 86 mg/100 ml to 73 mg/100 ml and thereafter remained constant. The level of serum FFA increased during the first 10 hr from an average value of 0.54 meq/liter to approximately 1.1. meq/liter and thereafter was relatively constant. Similar general trends occurred during treadmill walking; these are shown in Fig. 2. During the first 10 hr of testing, the serum level of glucose declined from 90 mg/100 ml to 66 mg/100 ml;

Fig. 1

Fig. 2

FFA increased from 0.70 meq/liter to an average level of 2.4 meq/liter. Our data obtained with working subjects show an increased variability with duration of treadmill walking. This was probably due, in part, to the decreasing number of subjects who were able to continue the test. For example, 16 subjects completed 16-1/2 hr of testing, but thereafter the number declined to 11, then 6, and finally 5.

To determine whether the changes in the blood levels of FFA and glucose during treadmill walking differed significantly from those measured during resting conditions, statistical comparisons were made between the steady-state levels, i.e., levels measured after 9 hr of testing. Generally, the level of serum glucose was 7.2 mg/100 ml lower during treadmill walking than during resting conditions ($t = 3.27$, $p < 0.05$). The level of serum FFA was 1.2 meq/liter higher during exercise ($t = 5.83$, $p < 0.05$).

The cumulative urinary creatinine and nitrogen excretion were examined during various phases of testing. Urinary creatinine tended to be slightly higher during treadmill walking. For example, after 15 hr of exercise, 17 subjects showed a cumulative excretion of 1.49 g of creatinine; during a comparable period of rest, the cumulative creatinine excretion was 1.26 g. These values differ significantly ($t = 3.66$, $p < 0.05$). The urinary total nitrogen excretion, on the other hand, was similar during both test conditions. These data are shown in Fig. 3. Fig. 3 After 15 hr of treadmill walking, the cumulative urinary nitrogen excreted was 8.14 g; during a comparable period of rest, the nitrogen excreted was 7.74 g. There is no significant difference in the means ($t = 1.59$, $p > 0.05$). Comparisons made after 18 and 20 hr of testing yielded essentially similar results.

A preliminary examination of the urinary ketone bodies excreted has been made. Under resting conditions, the average ketone excretion was 22 mg during every 1-1/2-hr period so that the cumulative ketone excretion increased linearly with the duration of testing. The average cumulative excretion in 24 hr was 346 mg. During the first 10 hr of treadmill walking, the ketone excretion was similar to the values measured during resting conditions; but thereafter the ketone excretion showed a tendency to increase markedly. There were, however, considerable individual variations. Some subjects walked for many hours and excreted 5-50 mg of ketone bodies during every 1-1/2-hr period; others excreted between 70-300 mg of ketones. Consequently, although the subjects who completed the treadmill test showed an average cumulative excretion of 1121 mg of ketones, no statistical significance can be demonstrated between the means obtained during working or resting conditions. There was no correlation between the urinary ketone body production and other physiologic parameters measured.

Hematocrit remained quite constant during both test conditions; the mean was 43%. The average body weight loss during treadmill walking was 2-1/2 lb. Similar changes in weight were observed in resting subjects.

DISCUSSION AND CONCLUSIONS

Energy metabolism in man has been examined in relation to prolonged periods of physical activity. The average energy deficit during the 24-hr period of resting was 1600 kcal. During treadmill walking, the average energy deficit was 5200 kcal with a maximum of 6800 kcal. The mean RQ during work was 0.74 which indicates that approximately 12% and 88%

of energy was derived from the oxidation of carbohydrate and fat, respectively. The RQ measured during resting conditions was not significantly different from the value measured during work. In our treadmill experiments, only 3-5% of total calories were derived from the metabolism of protein. Because of the close similarity of the serum and urinary levels of nitrogen during the working and resting state, we conclude that neither extensive protein breakdown nor the derivation of energy from protein is of consequence during work. This is in agreement with the results of other studies conducted with experimental dogs (32,33).

The present studies were designed to investigate certain biochemical characteristics associated with physical work. They followed closely an experimental work situation of 8-40-hr duration which has been developed with dogs to investigate the effect of food and water supplements (34,35), food deprivation (31), and the utilization of body energy reserves (32,33). In those studies with postabsorptive dogs, the blood lactate remained unchanged during treadmill running and the blood glucose at first declined then remained relatively constant for several hours. Under those conditions, physical exhaustion was not correlated with systematic changes in the blood chemistry. Our present observations confirm the finding of constancy of the blood lactate levels observed with dogs and more recently with man (25).

The tendency for serum glucose and FFA levels to stabilize after approximately 9 hr of testing is of particular interest. The reports of other researchers show a progressive decline in the level of blood sugar and a rise in the level of FFA during prolonged work with fasting

subjects. For example, recently Rodahl et al. (25) have studied the relationship of this characteristic to fatigue during work of 6-hr duration wherein the average energy expended was approximately 2300 kcal; they concluded, on the basis of declining levels of the blood glucose and rising levels of FFA, that the FFA/glucose ratio might serve as a useful index of exhaustion. Our studies, however, were of sufficient length for the establishment of steady-state levels for those blood components, and after approximately 9 hr of testing, the subjects maintained constant serum FFA/glucose ratios which were characteristic of the level of physical activity.

The factors which regulate the level of blood FFA are somewhat obscure. In our studies, the extent of calorie deficit was apparently not a relevant factor, since both the resting and working subjects showed similar time-dependent responses despite the much greater energy cost of physical work. With respect to fat utilization, some preliminary conclusions may be arrived at through a consideration of the levels of serum FFA in their relationship to the urinary ketone body production. For example, serum samples from resting subjects showed, somewhat surprisingly, a progressive rise in their levels of FFA during the first 9 hr of testing and finally reached relatively stable levels of approximately 1.1 meq/liter; the rate of urinary ketone body production, however, was not related to FFA level and was constant throughout the entire 24-hr period of observation. In working subjects, the serum FFA reached constant levels of 2.4 meq/liter which correspond to maximal levels reported in the literature. Before the FFA stabilized at that level, the urinary ketone body excretion of the working subjects was almost identical with the values measured during the resting state; thereafter, however, the

ketone body excretion of the working subjects, although quite variable, tended to rise. Therefore, it is suggested that serum levels of FFA in the neighborhood of 1.1-2.0 meq/liter can be maintained for considerable periods without excessive ketone body production, but that higher levels of the serum FFA are associated with increased ketone body excretion resulting from the incomplete metabolism of fats.

The rise in serum FFA, particularly in working subjects, is indicative of lipid mobilization. However, the extent to which the lipids are oxidized directly is not clear. Values stated in the literature indicate that 13-49% (16,29) of expended calories are derived from fat oxidation. In more recent studies with postabsorptive dogs, Issekutz and co-workers (18) estimate that 50% of the CO_2 produced from fat metabolism can be ascribed to the rapid oxidation of plasma FFA (palmitate-1C^{14}) during exercise. Inability to completely recover radioactive CO_2 from labeled palmitate led those authors to postulate extensive recycling phenomena which resulted in the incorporation of labile fatty acids into other body energy pools. We have made preliminary calculations to assess the loss of body fat and thus to estimate the amount of fat mobilized during work. On the basis of an average energy expenditure of 5200 kcal and an average nitrogen excretion of 9.3 g, our results indicate the loss of approximately 0.52 kg of fat. That amount of fat is trivial compared with the total body content. However, it is possible that the ability to sustain a high rate of lipolysis may be a critical factor which, in part, determines the extent to which FFA participate directly in energy-yielding reactions. It is interesting to note that during the phase of rising

serum FFA levels, the rate of FFA mobilization exceeds its utilization by the body. And whereas there is little doubt that nonepinephrine plays an important role in elevating the level of FFA during exercise, the factors which elevate FFA during the resting state are unknown. The eventual maintenance of steady-state levels of the FFA indicates the establishment of a balance between lipid utilization and mobilization.

In the absence of an exogenous source of carbohydrate, a gradual decline in the level of blood sugar was expected; however, stabilization of the levels of blood sugar for a prolonged period without apparent fatigue was not anticipated. Upon reaching steady-state levels, the glucose content of the serum samples from resting and working subjects differed by only 7 mg/100 ml. Because of the considerable differences in extent of calorie deficit in the two experimental situations, it is difficult to predict the factors which regulated the blood sugar levels. In working subjects, for example, it is likely that the initial decline in blood sugar level resulted from increased glucose utilization. In this regard, Goldstein (15) postulated the control of carbohydrate metabolism during exercise by a humoral hypoglycemic factor, distinct from insulin; he suggested that increased glucose oxidation was related to the influence of that factor upon cellular glucose transport systems. Therefore the eventual attainment of a steady-state level of blood sugar would require either a) a mechanism for the replacement of glucose during its rapid utilization, or alternately, b) a mechanism for the inhibition of glucose metabolism which in turn would serve to minimize the rate of extraction of glucose from the blood. Traditionally, the latter concept has enjoyed greater acceptance, and, usually, lowered levels of the blood

sugar are attributed to diminished glycogen reserves. Whereas that explanation seems appropriate in regard to conditions of physical exercise, we doubt its validity to explain similar changes in the level of blood sugar which were observed in the resting state. Consequently, we feel that further studies of the glycogen reserves and also of glucose utilization are required to more fully explain our findings.

Seldom is one in the position to measure physical capacity for work of long duration. In the present series, physical exhaustion was not conclusively related to the observed variations in the blood glucose and FFA levels during treadmill walking. However, it was possibly related to decreased efficiency of the cardiovascular system because, in most cases, we observed a slight increase in heart rate prior to the termination of the test. Then again, fatigue was possibly related to the deterioration of the neuromuscular system and higher mental processes since, on the one hand, loss of steadiness and incoherence of speech were persistent findings, and, on the other hand, emotional instability was occasionally noted. Still, for the most part, the subjects were highly cooperative and remained in good spirits during all phases of testing. One day of rest was required for full recovery from the fatigue experienced in treadmill walking.

Our results have demonstrated a qualitative similarity in many of the metabolic responses during prolonged work and prolonged rest. The general tendency in both experimental situations for the blood sugar

to decline and the FFA to rise during the first 9 hr of testing suggests a possible influence of undefined temporal factors on the body metabolism.

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REFERENCES

1. ARMSTRONG, D. T., R. STEELE, N. ALTSZULER, A. DUNN, J. S. BISHOP, and R. C. De BODO. Regulation of plasma free fatty acid turnover. Am. J. Physiol. 201:9-15, 1961.

2. BASU, A., R. PASSMORE, and J. A. STRONG. The effect of exercise on the level of non-esterified fatty acids in the blood. Quart. J. Exp. Physiol. 45:312-316, 1960.

3. BONSNES, R. W., and H. J. TRAUSSKY. Determination of creatinine. J. Biol. Chem. 158:581-589, 1945.

4. CARLSON, L. A., and B. PERNOW. Studies of blood lipids during exercise. I. Arterial and venous plasma concentrations of unesterified fatty acids. J. Lab. and Clin. Med. 53:833-841, 1959.

5. CARLSON, L. A., and B. PERNOW. Studies on blood lipids during exercise. II. The arterial plasma free fatty acid concentration during and after exercise and its regulation. J. Lab. and Clin. Med. 58:673-681, 1961.

6. CARLSON, L. A., L. EKELUND, and L. ORÖ. Studies on blood lipids during exercise. IV. Arterial concentration of plasma free fatty acids and glycerol during and after prolonged exercise in normal men. J. Lab. and Clin. Med. 61:724-729, 1963.

7. CHRISTENSEN, E. H., and O. HANSEN. III. Arbeitsfähigkeit und ernährung. Skand. Arch. Physiol. 81:160-171, 1939.

8. CHRISTOPHE, J., and J. MAYER. Effect of exercise on glucose uptake in rats and men. J. Appl. Physiol. 13:269-272, 1958.

9. COURTICE, F. C., and C. G. Douglas. The effects of prolonged muscular exercise on the metabolism. Proc. Roy. Soc. London. 119:381-439, 1936.

10. DIXON, W. J., and F. J. MASSEY, Jr. Introduction to statistical analysis. New York, McGraw-Hill Book Company, Inc., 2nd ed., 1957.

11. DOLE, V. P. A relation between non-esterified fatty acids in plasma and the metabolism of glucose. J. Clin. Invest. 35:150-154, 1956.

12. FISKE, C. H. and Y. SUBBAROW. The colorimetric determination of phosphorus. J. Biol. Chem. 66:375-400, 1925.

13. FOLIN, O., and H. WU. A system of blood analysis. J. Biol. Chem. 38:81-110, 1919.

14. FRIEDBERG, S. J., P. B. SHER, M. D. BOGDONOFF, and E. H. ESTES, Jr. The dynamics of plasma free fatty acid metabolism during exercise. J. Lipid Res. 4:34-38, 1963.

15. GOLDSTEIN, M. S. Humoral nature of hypoglycemia in muscular exercise. Am. J. Physiol. 200;67-70, 1961.

16. HAVEL, R. J., A.NAIMARK, and C. F. BORCHGREVINK. Turnover rate and oxidation of free fatty acids of blood plasma in man during exercise. Studies during continuous inclusion of palmitate-1-C^{14}. J. Clin. Invest. 42:1054-1063, 1963.

17. HENSCHEL, A., H. L. TAYLOR, and A. KEYS. Performance capacity in acute starvation with hard work. J. Appl. Physiol. 6:624-633, 1954.

18. ISSEKUTZ, B., Jr., H. I. MILLER, P. PAUL, and K. RODAHL. Source of fat oxidation in exercising dogs. Am. J. Physiol. 207:583-589, 1964.

19. JOHNSON, R. E., and R. PASSMORE. Interrelations among post-exercise ketosis (Courtice-Douglas effect), hydration, and metabolic state. Metabolism 9:443-451, 1960.

20. KIRK, P. L. Kjeldahl method for total nitrogen. Analytical Chem. 22:354-358, 1950

21. LOOMIS, M. E. An enzymatic fluorometric method for the determination of lactic acid in serum. J. Lab. and Clin. Med. 57:966-969, 1961.

22. MICHAELS, G. D., S. MARGEN, G. LIEPERT, and L. W. KINSELL. Studies in fat metabolism. I. The colorimetric determination of ketone bodies in biological fluids. J. Clin. Invest. 30:1483-1485, 1951.

23. MILLER, H., B. ISSEKUTZ, Jr., and K. RODAHL. Effect of exercise on the metabolism of fatty acids in the dog. Am. J. Physiol. 205:167-172, 1963.

24. REICHARD, G. A., B. ISSEKUTZ, Jr., P. KIMBEL, R. C. PUTNAM, N. J. HOCHELLA, and S. WEINHOUSE. Blood glucose metabolism in man during muscular work. J. Appl. Physiol. 16:1001-1005, 1961.

25. RODAHL, K., H. I. MILLER, and B. ISSEKUTZ, Jr. Plasma free fatty acids in exercise. J. Appl. Physiol. 19:489-492, 1964.

26. SAIFER, A., and S. GERSTENFELD. The photometric microdetermination of blood glucose with glucose oxidase. J. Lab. and Clin. Med. 51:448-460, 1958.

27. SAMUELS, L. T., R. C. Gilmore, and R. M. Reinecke. The effect of previous diet on the ability of animals to do work during subsequent fasting. J. Nutrition 36:639-652, 1948.

28. SOMOGYI, M. Determination of blood sugar. J. Biol. Chem. 160:69-73, 1945.

29. SPITZER, J. J., and M. GOLD. Free fatty acid metabolism by skeletal muscle. Am. J. Physiol. 206:159-163, 1964.

30. TROUT, D. L., E. H. ESTES, Jr., and S. J. FRIEDBERG. Titration of free fatty acids of plasma. A study of current methods and a new modification. J. Lipid Res. 1:199-202, 1960.

31. YOUNG, D. R. Effect of food deprivation on treadmill running in dogs. J. Appl. Physiol. 14:1018-1022, 1959.

32. YOUNG, D. R., and R. PRICE. Utilization of body energy reserves during work in dogs. J. App. Physiol. 16:351-354, 1961.

33. YOUNG, D. R., R. PRICE, N. E. ELDER, and R. R. ADACHI. Energy and eletrolyte metabolism and adrenal responses during work in dogs. J. Appl. Physiol. 17:669-674, 1962.

34. YOUNG, D. R., N. S. SCHAFER, and R. PRICE. Effect of nutrient supplements during work on performance capacity in dogs. J. Appl. Physiol. 15:1022-1026, 1960.

35. YOUNG, D. R., A. IACOVINO, P. ERVE, R. MOSHER, and H. SPECTOR. Effect of time after feeding and carbohydrate or water supplement on work in dogs. J. Appl. Physiol. 14:1013-1017, 1959.

TABLE 1. Physical characteristics of test subjects

Subject	Age, yr	Height, cm	Weight, kg	Pulse rate	Blood Pressure, systolic/diastolic
00	31	166.4	72.5	56	114/71
02	39	184.2	81.5	66	122/82
03	25	174.6	65.1	66	118/88
05	36	173.4	71.7	52	118/82
08	40	177.8	85.5	67	122/88
09	24	162.6	65.6	49	112/66
10	31	172.7	80.9	77	123/82
11	29	183.5	93.5	61	140/104
12	23	179.7	75.3	52	124/82
13	26	190.5	99.9	62	124/80
16	22	162.6	58.1	57	113/71
17	30	180.3	84.1	48	142/91
19	30	178.4	81.7	65	119/83
20	38	182.9	80.9	58	134/89
21	26	180.3	80.7	61	113/78
23	32	185.4	83.9	63	122/84
24	35	165.7	65.7	60	113/76
25	34	172.1	77.7	51	122/78
29	40	175.3	79.8	59	146/104
30	39	170.2	77.5	61	119/84

TABLE 2. Physiologic responses of postabsorptive subjects at rest and during treadmill walking

	Test conditions	
	Resting	Walking
O_2 Uptake, liters/min	0.280±0.37	1.130±0.09
% Peak effort*	7.82 ±0.93	31.7 ±2.14
Respiratory quotient	0.77 ±0.09	0.74 ±0.04
Heart rate/min	60.0 ±7.0	104.0 ±9.0
Rectal temperature, C	37.1 ±0.17	38.0 ±0.37
Serum NPN, mg/100 ml	28.1 ±3.70	28.1 ±3.09
Serum lactate, mg/100 ml	10.4 ±1.0	12.3 ±1.8
Serum sodium, meq/liter	144.0 ±1.9	145.0 ±2.0
Serum potassium, meq/liter	4.2 ±0.2	4.5 ±0.3
Serum phosphorus, mg/100 ml	3.7 ±0.4	4.3 ±1.3

*$\frac{\text{Observed } O_2 \text{ uptake} \times 100}{\text{Maximal } O_2 \text{ uptake}}$

Values are means ± standard deviations

ABSTRACT

Studies have been conducted to study postabsorptive energy metabolism under two levels of physical activity, resting or treadmill walking, for periods of up to 24 hr duration. During resting conditions, the serum glucose at first declined and then stabilized at a level of 73 mg/100 ml. The level of serum free fatty acids (FFA) reached a steady state level of 1.1 meq/liter. Similar trends occurred during treadmill walking, but they differed in magnitude. During work, the level of serum glucose declined to 66 mg/100 ml and thereafter remained constant: serum FFA reached a constant level of 2.4 meq/liter. The RQ, serum lactate, serum nonprotein nitrogen, and urinary nitrogen were similar during both test conditions. Under the conditions of the experiment a constant rate of influx and extraction of glucose as well as FFA from the blood was attained. Failure of other workers to attain steady state blood levels of FFA and glucose may explain the discrepancy of different investigations regarding FFA-glucose interrelationships during exercise.

INDEX TERMS

metabolism in work work, FFA, and glucose lipid and carbohydrate fatigue

FIGURE TITLES

Fig. 1- Serum free fatty acids (FFA) and glucose levels in resting postabsorptive subjects. Serum levels of glucose or FFA are shown on the ordinate. Duration of test in hours is shown on the abscissa. The 95% confidence interval for means is shown.

Fig. 2.- Serum free fatty acids (FFA) and glucose levels during treadmill walking in postabsorptive subjects. Serum levels of glucose or FFA are shown on the ordinate. Duration of test in hours is shown on the abscissa. The 95% confidence interval for means is shown.

Fig. 3.- Cumulative mean urinary nitrogen excretion at rest and during treadmill walking in postabsorptive subjects. The cumulative urinary nitrogen excretion in grams is shown on the ordinate. Duration of test in hours is shown on the abscissa. Resting subjects are designated by the open symbols; exercising subjects are designated by the closed symbols.

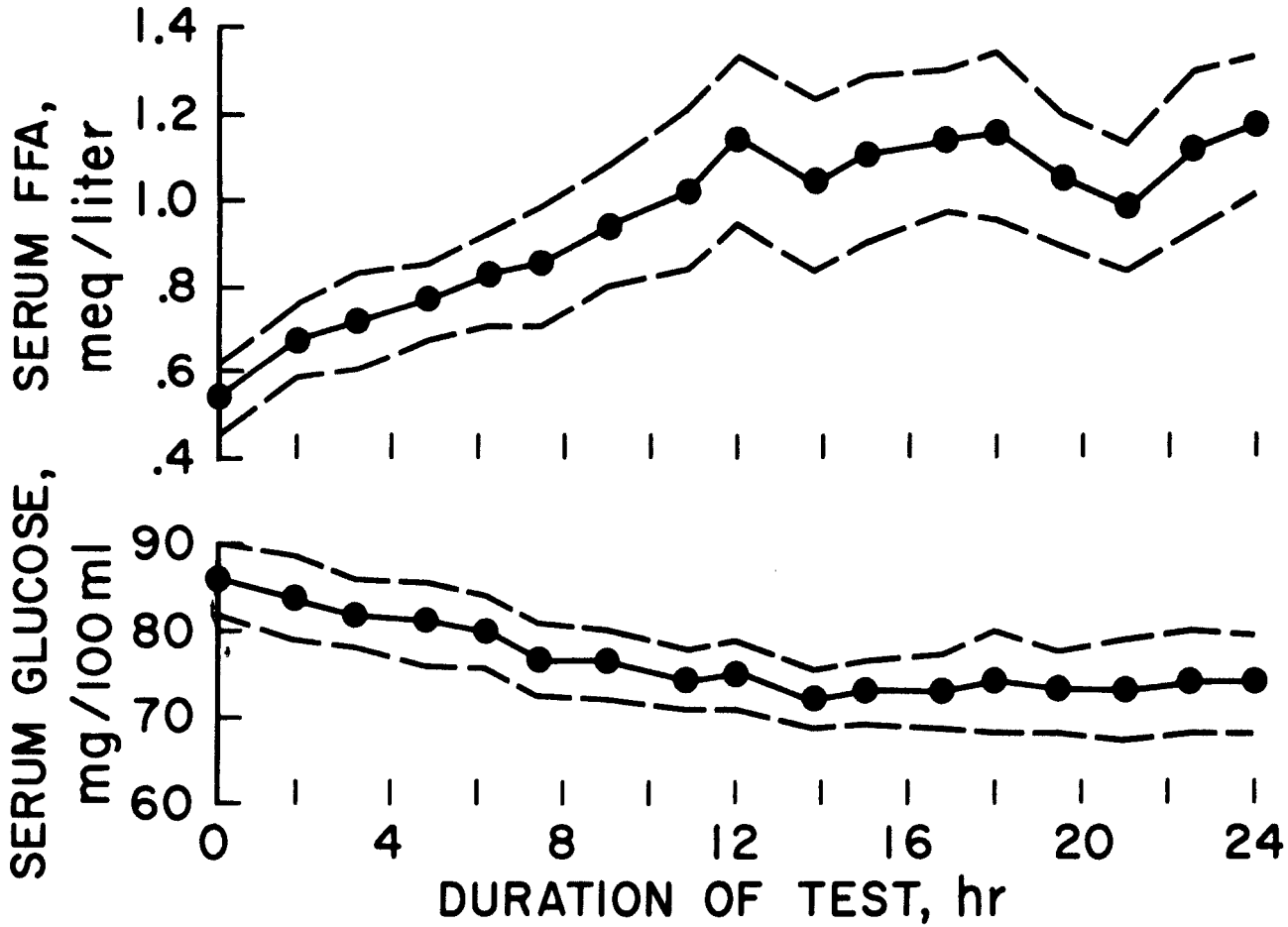

Fig. 1

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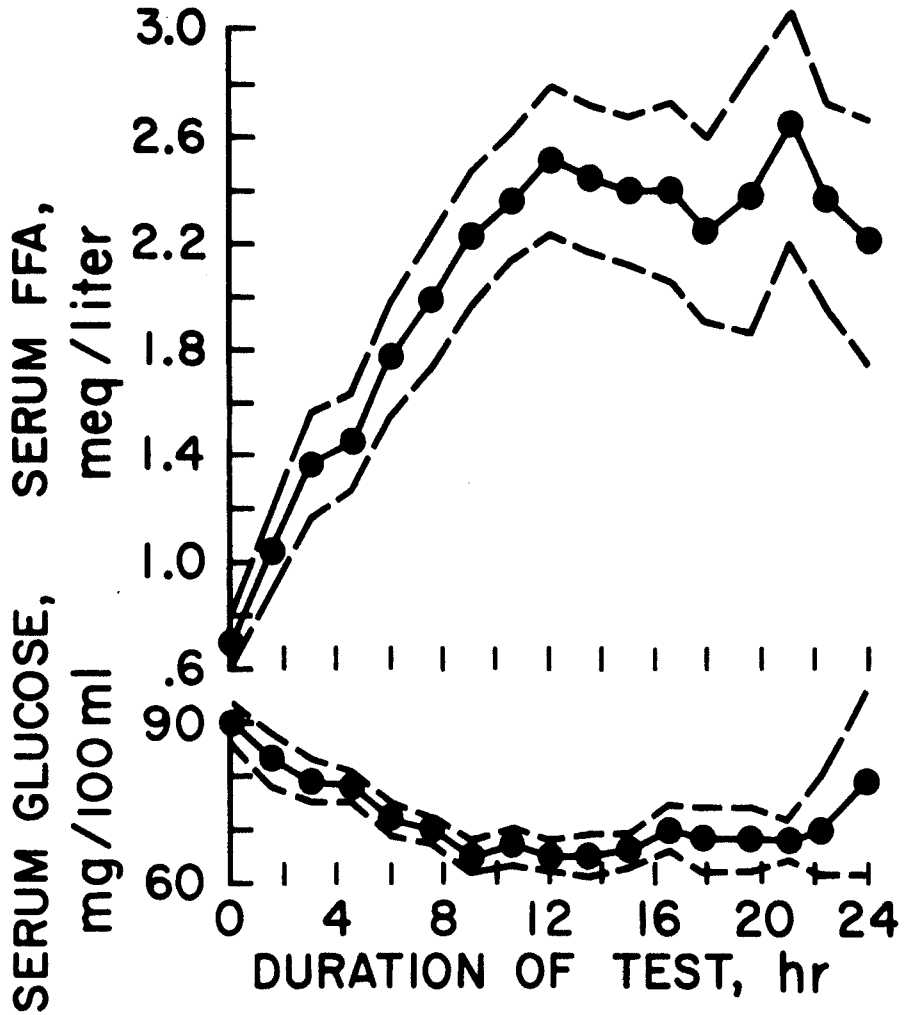

Fig. 2

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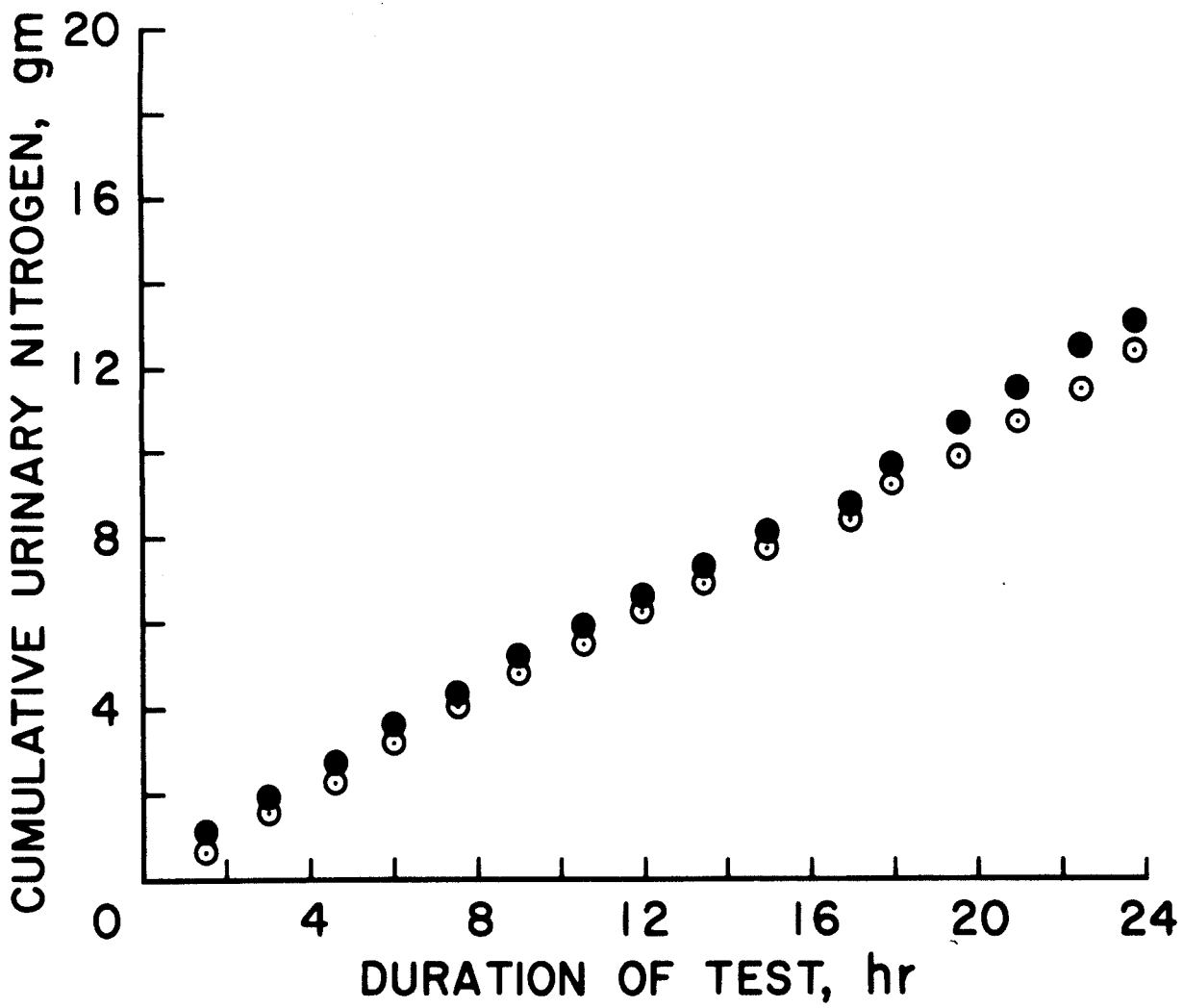

Fig. 3

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